# A Description of Five new Species of *Edwardsia*, Quatr., from New Guinea, with an Account of the Order of Succession of the Micromesenteries and Tentacles in the Edwardsidæ.

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(Plate 51, and 2 Text-figures.)

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For some time past I have been working out the anatomy of a collection of Anthozoa made some years ago by Dr. A. Willey in New Guinea. My apologies are due and are hereby tendered to him for not having undertaken this work sooner. For one reason or another it was put aside; but, when I began to give serious attention to it some eighteen months ago, I found that the collection included several forms of great interest, one of which I have already described. Among the specimens were five species of the genus *Edwardsia*, which form the subject of the present short memoir, and a number of other forms which appear to be related to, but can hardly be included in, the subfamily Phelliinæ. It was my intention to give a full and detailed description of the anatomy and histology of these forms, and I had expected to bring my work to a conclusion by the end of last summer. But my time has been taken up since the beginning of August by numerous interests arising from the European war, and, at the time of writing, I am about to leave Oxford for service in the Army. As my investigations on the Edwardsiæ were nearly complete, and the results partly written out in full, it has seemed desirable to put together, in however hurried a manner, such parts of my projected memoir as seem worth publishing as a preliminary notice. I have not been able, in the short time at my disposal, to give an account of my observations on the anatomy and histology of the species I have studied, and this must be deferred to a future publication. The present paper is confined to a description of the five species collected by Dr. Willey in New Guinea, and to an account of the sequence of the development of the tentacles and micromesenteries in the Edwardsiæ.

The genus *Edwardsia*, de Quatrefages, has been the subject of much discussion among actinologists in recent years, and has successively been raised to the rank of an ancestral type and degraded to the position of a degenerate offshoot of the dodecamerous Actinians. It was originally described by de Quatrefages (23), O. & R. Hertwig (15), and Andres (1) as having eight, and only eight, mesenteries, of which the muscle-banners are arranged on a plan exactly resembling that of the first four couples of protocnemes of Actinians and Corals. This feature attracted the special

notice of Boveri (5) and McMurrich (18, 19, 20) ; and these two authors, by ingenious and convincing arguments, showed that the various plans of mesenterial sequence exhibited by the Cerianthidæ, Zoanthidæ, Antipatharia, Madreporaria, and Actiniidea could be derived from the Edwardsian type, and claimed that the existing Edwardsidæ are to be regarded as the ancestral type from which all the groups enumerated have been evolved. But in 1895 Faurot (10) showed that, in addition to the large macromesenteries with conspicuous muscle-banners, a variable number of micromesenteries, confined to the upper region of the capitulum, and so small as to have escaped previous notice, exist in the two species *E. beautempsii* and *E. adenensis*. In the former species the positions of the micromesenteries could be compared with the arrangement seen in *Halcampa*, and it was therefore no longer possible to regard *Edwardsia* as an ancestral type. The late Prof. Ed. van Beneden discussed the relationships of the Edwardsidæ in his splendid memoir on the Anthozoa of the Plankton Expedition (3), and argued that they are Hexactinarians simplified by progressive regression of the mesenteries of the second cycle and of the fifth and sixth mesenterial couples of the first cycle. He added : " Au surplus il faut renoncer à voir dans les Edwardsiés le type ancestral d'où seraient issus les Hexactiniaires." Van Beneden's view of the relationship of the Edwardsidæ has been generally adopted, and for the last eighteen years they have been classified among the Actiniaria, and as early as 1898 Carlgren (8) classified them together with the Halcampomorphidæ in his subtribe Athenaria, which corresponds very nearly to the family Ilyanthidæ of Gosse.

It is not possible for me, at the present juncture, to enter into a discussion of the very debateable questions of the classification of the Anthozoa. It is sufficient for me to state that I accept the principle of Carlgren's (9) division of the Anthozoa into the three subclasses Hexacorallia, Octocorallia, and Dodecacorallia, but cannot reconcile myself to the use of the names proposed. Carlgren's Hexacorallia includes the Cerianthidæ and the Antipatharia, and is equivalent to van Beneden's group Ceriantipatharia. The classification seems a natural one, but as the Actinians and Corals have long been known as Hexactiniæ and it is now desired to insist on the separation of the Cerianthidæ from these forms, Carlgren's choice of a name seems to me unfortunate and liable to cause confusion. The Ceriantipatharia of van Beneden are a subdivision of the " Scyphactiniaria," a subclass including the Scyphomedusæ and Rugosa. In my opinion there are valid reasons for excluding the Scyphomedusæ from the Anthozoa, and the position of the so-called " Rugose " Corals is still uncertain. I am inclined to use van Beneden's name of an order, Ceriantipatharia, for the name of a subclass, identical with Calgren's Hexacorallia and equivalent in rank to the Octactiniaria and Zoanthactiniaria. The last name is van Beneden's, and is equivalent to Carlgren's Dodecacorallia. The sub-

class includes the orders Zoantharia, Carlgren (= Zoanthinaria, van Beneden), and Hexactiniaria, van Beneden, the last-named comprising the Actiniaria and Madreporaria. As it is the purpose of this paper to show that the Edwardsidæ have not the character of six pairs of first-cycle mesenteries indicated by the names "Hexactiniaria" and "Dodecacorallia," I cannot accept either Carlgren's name for the subclass or van Beneden's name for the order which is to include the Edwardsidæ. I think that van Beneden's name, Zoanthactiniaria, may well stand for the subclass named Dodecacorallia by Carlgren. This subclass, according to my opinion, comprises three orders—the Edwardsiaria, the Zoanthinaria (= Zoantharia, Carlgren), and the Dodecactiniaria, the last-named comprising the suborders Actiniaria and Madreporaria, or, as I have called them in another place (4), and still prefer to call them, the Malacactiniæ and Scleractiniæ.

It is the object of the latter part of this paper to justify my opinion that the Edwardsiaria form a group distinct from, and of equal rank with, the Zoanthinaria and the Dodecactiniaria.

## I. *Description of new Species.*

### Subclass ZOANTHACTINIARIA, van Bened.

### Order EDWARDSIARIA, mihi.

### Family EDWARDSIDÆ, Andres.

### Genus EDWARDSIA, de Quatrefages.

EDWARDSIA MAMMILLATA, n. sp. (Plate 51. fig. 1.)

Body clearly divided into capitulum, scapus, and physa. Scapus about four-fifths of the entire length of the animal, covered by a thick olive-green epidermis, transversely wrinkled, studded with eight longitudinal rows of elevated semi-transparent tubercles of various sizes; the largest tubercles mammilliform and situated at about a quarter of the whole length of the scapus from the capitular end, thence diminishing in size towards the physa; the tubercles intermesenterial in position. Capitulum when contracted about one-twentieth the length of the scapus, colourless in spirit, its surface divided into eight intermesenterial areas by shallow grooves corresponding to the insertions of the macromesenteries; its upper border thickened and raised into ten more or less triangular elevations which, in a contracted specimen, overhang the edge of the infolded oral disc and alternate with the bases of the tentacles. Physa about as long as the capitulum, acorn-shaped, tapering posteriorly, colourless, transversely wrinkled, without epidermis or tubercles, with a terminal depression resembling a terminal pore. Tentacles ten in number, short, conical, in contraction infolded over the oral disc.

Macromesenteries eight, with well-developed parietal muscles and moderately well-developed longitudinal retractor muscles; the mesoglœal folds forming the muscle-banners 10–13 in number, slightly branched. Micromesenteries two, one in each lateral macromesenterial interspace, small, without retractor muscles, confined to the capitulum.

Length of contracted specimen, 13–14 mm.; diameter, 1 mm.

*Hab.* Ile du Phare, Nouméa, New Caledonia.

Edwardsia rugosa, n. sp. (Plate **51**. fig. 2.)

Body divisible into capitulum, scapus, and physa. The capitulum not distinctly marked off, finely wrinkled transversely, with eight longitudinal shallow furrows corresponding to the insertions of the macromesenteries, covered with a very thin epidermis. The scapus coarsely wrinkled transversely and covered with warty tubercles somewhat irregularly arranged in eight longitudinal rows, the tubercles in the upper part of the scapus tending to form double rows, and some scattered in the intervening areas between the rows. The whole scapus invested by a thin bright ochreous-brown epidermis. The physa globose, colourless, without epidermis, with a very distinct terminal depression resembling a terminal pore.

Length, 35 mm.; greatest diameter, 3 mm.

*Hab.* Sariba, China Straits, British New Guinea.

The single specimen on which this species is founded had apparently undergone a considerable amount of decomposition before being placed in spirit. The external characters were fairly well preserved, but the internal organs, the tentacles, oral disc, and actinopharynx were so much macerated that I was unable to count the tentacles, to recognize any micromesenteries, or determine the extent and characters of the actinopharynx. The macromesenteries were so far recognizable in sections that I could determine the existence of the eight "Edwardsian" mesenteries with well-developed parietal muscles, and large muscle-banners with the characteristic orientation. In the débris of the tissues I could distinguish a few ova. The animal was therefore sexually mature, and there can be no doubt that it is a member of the genus *Edwardsia*. The colour and consistency of the thin friable epidermis, the nature of the transverse rugæ of the scapus, and the arrangement of the tubercles in irregular longitudinal rows offer sufficiently distinct characters to justify my describing this specimen as a separate species. The globose physa is also a marked feature, and, as is shown in fig. 2, it presents a circular and rather deep terminal depression; but I could not find any evidence in longitudinal sections of a pore leading into the cœlenteron.

I think I am correct in describing the finely-wrinkled slightly-swollen upper end of the specimen as a capitulum; it is fairly distinctly marked off from the rest of the scapus, but it may be only a somewhat modified upper

part of the scapus. There was no other structure at the oral end that I could identify as a capitulum ; but the tissues within the involuted oral end were so much macerated that it was impossible to come to a definite conclusion on the matter.

EDWARDSIA VERMIFORMIS, n. sp. (Plate **51**. fig. 3.)

The animal vermiform, tapering towards the oral extremity, thickest in the middle and tapering again towards the posterior extremity, where it expands rather abruptly to form the large, ovoid, thin-walled physa. No distinguishable capitulum. The two tapering ends of the scapus marked with eight longitudinal shallow grooves corresponding to the insertions of the macromesenteries, and furrowed at intervals by transverse wrinkles so regularly disposed as to give an appearance of segmentation ; the thicker middle portion of the scapus devoid of longitudinal furrows and transverse wrinkles. The whole scapus covered by a thin, very minutely wrinkled, yellowish-brown epidermis, easily rubbed off and showing a slaty-grey mesoglœa below. The physa thin-walled, saccular, compressed, without longitudinal and transverse grooves. Colour in spirit : scapus a dirty olive-grey, physa a dull orange.

Length, 36 mm. ; greatest diameter, 5 mm.

*Locality*. Uvea, Loyalty Islands.

The single specimen on which the above description is founded was in an even worse state of preservation than *E. rugosa*. I could find no trace of tentacles, oral disc, or actinopharynx in sections. The eight macro-mesenteries were partially preserved, and I was able to identify the muscle-banners, which were evidently large, with complicated much-branched mesoglœal folds. The swollen condition of the middle third of the body is due to the presence of the large muscle-banners. The physa was flattened and surrounded by a deep fold, which was probably due to compression in packing. When dilated, the physa must have been of unusually large size in proportion to the rest of the animal. There are no verrucæ visible to the naked eye on the scapus ; but examination with a lens and sections showed that many of these highly characteristic Edwardsian structures are scattered over the areas between the longitudinal grooves of the scapus. There is no doubt that this specimen is an *Edwardsia*, very different from the other species in Dr. Willey's collection, and I cannot refer it with certainty to any described species, so I describe it provisionally as a new species. It is somewhat similar to Klunzinger's (16) figure of *E. pudica*, Klg., but the physa of the latter is much narrower and tapers towards the posterior extremity. This difference may be due to the different states of contraction of the animals from which his figure and mine were drawn, and it is possible that the two species may eventually prove to be identical.

Edwardsia rakaiyæ, n. sp. (Plate 51. fig. 4.)

Scapus sepia-brown in colour, divided into eight longitudinal areas by as many well-marked grooves, corresponding to the insertions of the eight macromesenteries. The whole scapus irregularly rugose or papillate, the rugæ and papillæ forming indefinite transverse rows; the papillæ smaller in the grooves, larger in the longitudinal areas between, where they have a warty appearance and are minutely studded with greenish-white vesicles. The distal fifth of the scapus introversible. Capitulum very short, colourless in spirit, with twenty faint longitudinal grooves corresponding to the insertions of the macro- and micromesenteries. Physa oviform, colourless, without longitudinal grooves and raised intervening areas, separated by a well-marked constriction from the scapus. Tentacles twenty in number, colourless in spirit, 6–7 mm. long in contracted condition, tapering, in contracted specimens usually infolded and crowded together in the bottom of the invaginated part of the scapus, but some may be wholly or partially invaginated. The tentacles in two circlets—the inner comprising eight, the outer twelve tentacles.

The eight macromesenteries extend from the oral disc to the physa; their longitudinal retractor muscles are enormously developed in the region of, and immediately below, the actinopharynx, where they form eight prominent muscular rolls, but tapering rapidly aborally and ending in thin strands in the physa. Micromesenteries minute, confined to the capitulum, incomplete, with parietal but without longitudinal retractor muscle-fibres, twelve in number, two in each sulco-lateral, lateral, or sulculo-lateral intermesenterial interspace. The actinopharynx short, without a differentiated sulcus or sulculus. A distinct band-shaped endodermic sphincter muscle at the junction of the capitulum and physa.

Length of contracted specimen, 76 mm.; length of the physa, 5 mm.; greatest diameter, 10 mm.

*Hab.* Straits of Rakaiya, New Britain.

The three specimens of this species were fairly well preserved, and I was able to study the anatomy in some detail, both by dissection and in sections. But, owing to the contraction of the very powerful retractor muscles, all the specimens were burst and their shape more or less altered and distorted. In all of them a longer or shorter section of the scapus was introverted, in addition to the capitulum, this being a normal occurrence in *Edwardsia* and described by Gosse for *E. beautempsii* (*callimorpha*, 11, p. 257). In the specimen selected for illustration (Pl. 51. fig. 4) the scapus has given way a short distance below the point of introversion, and the lower portion has shrunk back, leaving a portion of the inner wall of the introverted portion exposed. In the two other specimens the scapus had given way below the actinopharynx, and the large retractor muscles projected from the gap thus torn in the body-wall.

EDWARDSIA WILLEYANA, n. sp. (Plate 51. fig. 5.)

Scapus not divided into areas by longitudinal grooves corresponding to the insertions of the macromesenteries, but invested by a bright chestnut-brown epidermis marked by numerous, fine, transverse rugæ and studded with numerous, colourless, more or less elevated, rounded vesicles or papillæ arranged in numerous, irregular, longitudinal rows. No distinct physa, but the body tapers towards the posterior extremity and forms a blunt cone on which the epidermis is very thin and the papillæ more closely crowded together. The capitulum very short, its surface marked by eight deep grooves corresponding to the insertions of the macromesenteries, the areas between the grooves tumid and raised at the edge of the oral disc into eight more or less pointed, marginal tubercles alternating with the bases of the outer circlet of tentacles. Tentacles sixteen in number, arranged in two circlets of eight each ; the tentacles subulate, very extensile ; in a retracted specimen some are simply infolded over the oral disc, others are partially or wholly invaginated. Eight macromesenteries extending from the oral disc to the posterior extremity, their retractor muscles highly developed in the region of and below the actinopharynx, but tapering abruptly to form mere strands of muscular fibres posteriorly. Micromesenteries very minute, with well-developed parietal muscles but no retractors, eight in number, two in each sulculo-lateral, one in each lateral and sulco-lateral macromesenterial interspace. Actinopharynx short, sacculated, with a distinct sulcus and sulculus. No definite sphincter muscle.

Length of contracted specimen, 40 mm. ; greatest diameter, 6 mm.

*Hab.* Straits of Rakaiya, New Britain.

In this single specimen of *E. willeyana* seven macromesenteries extend to the aboral end, one of the eight being shorter than the others. The aboral end is perforated by seven distinct pores leading into the seven aboral intermesenterial spaces. These pores are not visible externally in the spirit-preserved specimen, but can easily be demonstrated in sections. The detailed account of the situation and structure of these pores must, however, be deferred to a future paper.

## II. *The Order of Succession of the Tentacles and Micromesenteries in the Edwardsidæ.*

I have been able to study the positions of the mesenteries and the relations of the tentacles to the intermesenterial chambers in six species of *Edwardsia* with some degree of exactitude. In these species the number of tentacles varies from ten in *E. mammillata* to thirty-two in *E. carnea*. In every case the number of mesenteries is the same as the number of tentacles—in other words, each tentacle corresponds to an intermesenterial chamber.

Other observers have given more or less detailed accounts and figures of the relations of the tentacles to the mesenteries in various species of *Edwardsia*; and, comparing their work with my own, it seems that the mesenteries and tentacles are formed in a regular and, on the whole, consistent sequence, which I shall attempt to describe in the following pages. Unfortunately, very little is known of the development of the Edwardsiæ, and in no case has the order of appearance of the micromesenteries and tentacles been determined. The youngest larvæ described have the eight primary macromesenteries fully developed.

Probably the youngest larva that has been studied is the one described as no. iv. of the larvæ with eight mesenteries by E. van Beneden (3). This larva was not identified as an *Edwardsia*, but it has all the appearance of belonging to that genus. It was ovoid in shape, without tentacles or buccal cone, and had the eight characteristic "Edwardsian" mesenteries, each provided with a large and prominent reniform muscle-banner. Boveri (5) obtained larvæ of similar character; in the youngest stage they were spheroidal and apparently without tentacles, but one of them was reared in an aquarium for three months and at the end of that time was 1 cm. long and showed Edwardsian characters, agreeing in colour and form with *E. claparedii*, but had only eight tentacles.

Meyer and Möbius (17) in 1863 obtained many specimens of *E. duodecimcirrata* (= *E. lütkeni*) with from eight to eleven tentacles, but only figure one with nine tentacles. From this figure it appears that the insertions of the mesenteries on the peristomial disc were marked by radiating lines of colour, as is usual in Edwardsiæ, and it is evident that the eight Edwardsian mesenteries are present and that an additional mesentery has been formed, probably in one of the lateral chambers. A single tentacle corresponds to each mesenterial chamber. With these may be compared the parasitic larva of *Halcampa chrysanthellum*, fully described and carefully figured by Haddon (13). This larva has six pairs of Hexactinian mesenteries, but only eight tentacles, and it is noteworthy that, with the exception of the two corresponding to the directive endocœles, all the tentacles are exocœlic; no tentacles are as yet formed in the dorso-lateral and ventro-lateral endocœles.

Putting this information together, it is evident that in the larval *Edwardsia* and also in the larval *Halcampa* the first tentacles to appear—which I shall henceforth call the primary tentacles—are formed as prolongations of the eight primary chambers into which the cœlenteron is divided by the eight so-called Edwardsian mesenteries. For convenience of description, these eight chambers may be called megacœles. It should be noted that in Hexactinians two of these tentacles—namely, those of the directive megacœles—become endocœlic, six become exocœlic, and, as Faurot (10) has shown in the case of *Ilyanthus parthenopæus*, these six are

the only exocœlic tentacles until three cycles of endocœlic tentacles are completed, when fresh tentacles are formed in the remaining exocœles, making, with the six primary tentacles, the full complement of twenty-four.

The next step is shown by my specimen of *E. mammillata*. This specimen is probably adolescent, and the secondary tentacles are just beginning to be formed. Here, as is shown in text-fig. 1, a micromesentery has been formed in each lateral megacœle. These micromesenteries correspond in position with the fifth couple formed in Hexactinian development, and might be considered homologous with them; but in none of the specimens I have examined do they bear any trace of longitudinal muscle-banners, and, as I shall show in the sequel, there is no evidence to warrant our attempting to make an exact homology between the micromesenteries of Edwardsidæ and the last two couples of the first cycle and the succeeding pairs of mesenteries in Hexactiniæ. As regards the tentacles in *E. mammillata*, it is obvious from text-fig. 1 that the two directives, and the tentacles on each side of them, are primary tentacles and prolong the two directive and the two dorso-lateral and ventro-lateral megacœlic chambers. In each lateral chamber there are two tentacles separated by the micromesentery. I was not able to determine the point with certainty, but, so far as I could judge, the more dorsal of the two tentacles in each of these chambers was the smaller and situated nearer the edge of the disc than the rest. If this be indeed the case, the ventral tentacle in each chamber is the primary, the more dorsal a newly-formed secondary tentacle. As a rule, the primary tentacle is dorsal, the secondary tentacle ventral in the lateral chambers; but in this matter *E. mammillata* agrees with *E. claparedii*.

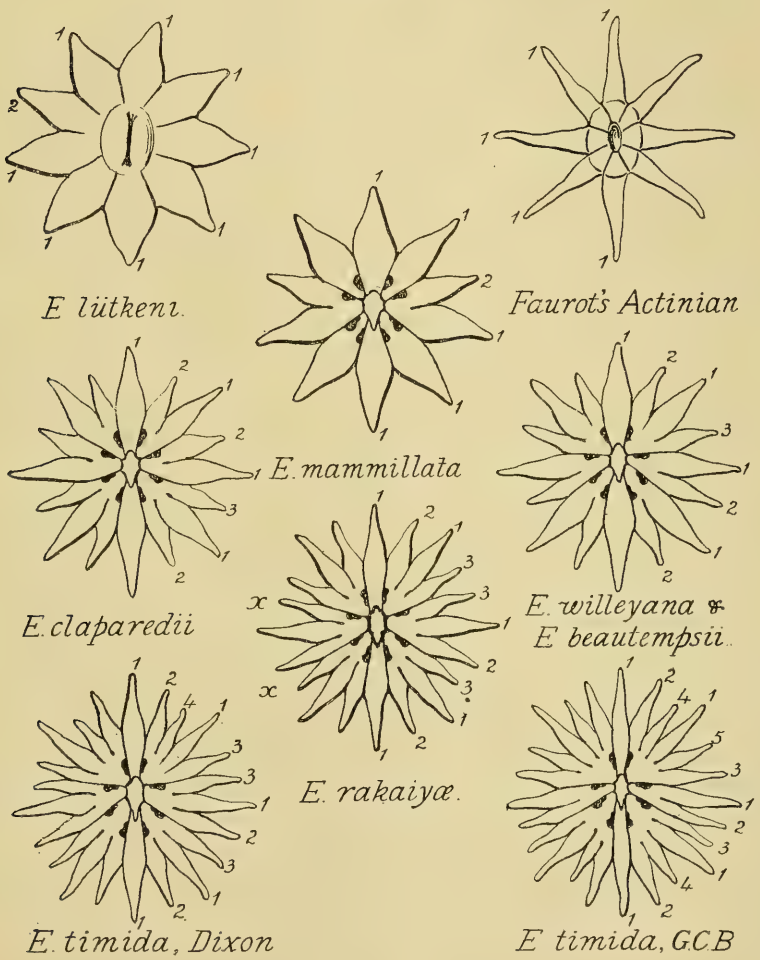
Specimens of species of *Edwardsia* with 11–15 tentacles have been mentioned by various authors, but none of them has been studied in detail. Therefore, we must pass on to forms with sixteen tentacles, of which four species are known—*E. claparedii*, *E. beautempsii*, *E. willeyana*, and *E. adenensis*. The first of these differs in some respects from the next two, and, as I shall show, *E. adenensis* is evidently an adolescent form of a species which has a larger number of tentacles when adult. *E. claparedii* has been thoroughly described by Andres (1). Of the sixteen tentacles, two are directives, two belong to each dorso-lateral megacœle, two to each lateral megacœle, and three to each ventro-lateral megacœle (text-fig. 1). They are alternately long and short, and Andres' figure shows clearly that the more ventral tentacle in the dorso-lateral and lateral megacœles is the primary, but the middle tentacle of the group of three in the ventro-lateral megacœle is the primary. Andres's figure also shows the eight micromesenteries, but he failed to realize their character and makes no mention of them.

*E. beautempsii*, described in detail by Faurot (10), and *E. willeyana* have the same number and arrangement of micromesenteries and tentacles, but differ from *E. claparedii* in the following respect: there are three tentacles in each of the dorso-lateral megacœles, the middle one of the group of three being the largest and obviously the primary tentacle. There are two tentacles in each of the lateral and ventro-lateral megacœles, and in each case the larger and more centrally placed primary tentacle is on the ventral side of the chamber, not on the dorsal as in *E. claparedii*. Evidently the precise order of the appearance of the micromesenteries and tentacles in the megacœles is liable to some variation within the limits of the genus; and it is just this variation that negatives any attempt to homologize the micromesenteries that first arise in the lateral and ventro-lateral megacœles of the Edwardsiæ with the fifth and sixth couples of the first cycle of Hexactinian mesenteries. Were the order of appearance always the same as it is in *E. claparedii* (and possibly in *E. mammillata*) the homology would be justified; for in this species the primary tentacle remains in what in a Hexactinian would be an exocœle, and the new secondary tentacle is formed in what in a Hexactinian would be an endocœle, and thus far the order of succession would be exactly analogous to what has been recorded by Faurot (10) for *Ilyanthus parthenopæus* and by Haddon (13) for *Halcampa chrysanthellum*. But the different order of succession in *E. willeyana* forbids our extending this homology to the whole genus. In this species (and also in *E. timida*, as I shall show further on), in both the lateral and ventro-lateral megacœles, the primary tentacle remains in what in a Hexactinian would be the endocœle, and the newly-formed secondary tentacle is in the exocœle. Further, when new micromesenteries and tentacles are added, as is the case in *E. timida*, they arrive on the *dorsal* side of the primary tentacles (text-fig. 1), and therefore in what in a Hexactinian would be the endocœles. Thus a fundamental rule of the succession of mesenteries in Hexactinians would be violated. The conclusion is that the mesenteries in question in the Edwardsiæ are not homologous with, and certainly not homogeneous in the sense of being derived by descent from, the fifth and sixth couples of the first cycle of Hexactinian mesenteries.

In *E. rakaiyæ* there are twenty mesenteries (eight macromesenteries and twelve micromesenteries) and twenty tentacles, disposed in a very regular manner, as is shown in text-fig. 1. In this species it is sufficiently obvious that the eight larger primary tentacles form the inner cycle, and that it is the primary tentacle that occupies the central position in the group of three occupying each of the dorso-lateral, lateral, and ventro-lateral megacœles. It follows from this arrangement that the tentacles do not alternate as in *E. claparedii* and *E. willeyana*, but that there are four pairs of contiguous outer cycle tentacles—one member of each pair on either side of the dorso-lateral and ventro-lateral macromesenteries. In this species there is no

evidence available to show whether the secondary tentacles appear on the dorsal or ventral side of the primary tentacles in the lateral and ventro-lateral megacœles. I am inclined to the opinion that they appear, as in *E. willeyana*, on the ventral side, but chiefly because, if they do, the case of *E. adenensis* meets with a ready explanation. For if, after sixteen tentacles

Text-figure 1.




have been established in this species, tertiary mesenteries arise forming the microcœles marked *x*, *x* in text-fig. 1, but the tentacles corresponding to these microcœles are retarded in development, we get precisely the condition described by Faurot for *E. adenensis*, a species which has hitherto been regarded as an exception, because it has a greater number of mesenteries

than tentacles. I think there can be no doubt that Faurot's specimen had not attained its full growth and full complement of tentacles. In the two living specimens of *E. timida* kept under careful observation by G. Y. Dixon (6) there were respectively 20 and 22 tentacles. In both specimens of this species that I studied by means of sections there were twenty-four tentacles and twenty-four mesenteries. Dixon's specimen with twenty tentacles, referred to by him as $\beta\beta$, was abnormal ; but his specimen with twenty-two tentacles exhibits an arrangement perfectly consistent with what I have observed. In Dixon's $\alpha\alpha$ specimen the arrangement of the tentacles is the same as in *E. rakaiæ*, but a quaternary tentacle has made its appearance on the dorsal side of the primary tentacle in each of the dorso-lateral megacœles. At least, this is what I surmise has taken place, because in both my specimens of *E. timida* the largest number of tentacles and mesenteries is in this megacœle—so I have taken the liberty to reverse Dixon's figure. He only studied the living animal, and could not tell, except by sections, which was the dorsal and which the ventral aspect of the animal.

In my two specimens of *E. timida* the tentacles are twenty-four in number, and there are the usual eight macromesenteries and sixteen micromesenteries. As studied in sections, the tentacles are obviously of different lengths, and, though the relative lengths are not always a safe guide to the age of tentacles in Actinians, I do not think I am wrong in assuming that the conspicuously longer and larger tentacles in these specimens were formed earlier than the shorter and smaller, especially as both specimens give the same results in this respect. Each of the directive megacœles is prolonged, as usual, into a single primary tentacle. The dorso-lateral megacœle gives off five tentacles, of which the two outermost, respectively nearest the dorsal and dorso-lateral macromesenteries, are conspicuously longer than the others. Within them are two very short tentacles and in the centre a long tentacle, which is clearly the primary. The probable order of appearance of these tentacles is indicated by the numerals in text-fig. 1. In each lateral megacœle there is only a single micromesentery separating two unequally-sized tentacles. Of the latter the dorsal is decidedly the longer, and must be identified with the primary tentacle. My specimens have therefore a smaller number of mesenteries and tentacles in the lateral megacœles than Dixon's, though more advanced in other respects. In the ventro-lateral megacœles there are three mesenteries dividing the peripheral part of the megacœle into four microcœlic chambers, from each of which issues a single tentacle. That nearest the ventral directive is large ; the next one to it is small ; then follows a large tentacle ; then a small one, next to the ventro-lateral macromesentery. In this chamber it is obvious that a quaternary tentacle has been formed on the ventral side of the primary.

Since writing the above, I have had the opportunity of studying a single example of *Edwardsia beautempsii*, de Q., and five examples of *E. carnea*, Gosse, sent to me from Plymouth by the Director of the Marine Biological Station. I kept these animals alive in an aquarium for some time, in the hope that I might obtain larvæ; but, failing to observe any signs of reproduction, I killed and made sections of them. As regards *E. beautempsii*, I have nothing to add to Faurot's account of the anatomy. The five examples of *E. carnea* were often ensconced in holes bored by *Saxicava* in a small piece of limestone. It was impossible to extract them from their holes without injury; so all five had to be killed at one operation, and only three were sufficiently well preserved in an expanded condition to admit of microscopical examination. I will refer to these three as specimens A, B, and C.

A had 24 tentacles—one in each of the dorsal and ventral directive megacœles, three in the dorso-lateral, three in the ventro-lateral, and four in the lateral chambers on each side of the body.

In specimen B there were thirty tentacles, disposed as follows:—One in each of the dorsal and ventral directive megacœles; four in each of the lateral and ventro-lateral megacœles; on the right side of the body (left in the drawing) five in the dorso-lateral megacœle, and seven in the corresponding megacœle on the left side of the body. In this specimen, therefore, growth had proceeded more rapidly in the left dorso-lateral megacœle than in the right.

In specimen C there were thirty-two tentacles: five in each dorso-lateral megacœle, six in each lateral megacœle, four in each ventro-lateral megacœle, and the two dorsal and ventral directive tentacles.

It is a good example of the irregularity of growth in Edwardsias that in A and C the largest number of tentacles and mesenteries is in the lateral megacœles, but in B in the dorso-lateral megacœles. In the living animals, when fully expanded, no appreciable difference in the length of the tentacles could be detected; but in all the five specimens, when expanded and in repose, every alternate tentacle was held straight out in radial fashion and the intervening tentacles were curled inwards towards the oral disc. So far as I could determine, the dorsal and ventral tentacles were always curled inwards.

It was impossible to judge of the age of the tentacles by their lengths in *E. carnea*; but in specimen B, which was killed in a fully expanded condition, I was able to observe that the micromesenteries were of different lengths, and as the number of tentacles and micromesenteries in the dorso-lateral megacœles of this specimen was different, it afforded an excellent opportunity of forming a judgment as to the order in which the micromesenteries and tentacles were developed. Text-fig. 2, which is founded on a combination of a series of transverse sections, shows that in the right

(left in the figure) dorso-lateral megacœle the two micromesenteries adjacent to macromesenteries extend nearly across the peristome to the actinopharynx, the two micromesenteries in the middle of the chamber are shorter, but that on the dorsal side is markedly the shorter of the two. In the corresponding megacœle on the left side of the body (right in the figure) there are six micromesenteries, of which the two adjacent to the macromesenteries are the longest, the two in the middle of the chamber are very short, and the two others are of intermediate length. In each of the lateral and ventro-lateral

Text-figure 2.


1. Oral disc of a specimen of *Edwardsia carnea*, Gosse, with 30 tentacles, eight macromesenteries, and twenty-two micromesenteries.

2–5. Diagrams of one of the dorso-lateral megacœles, showing the probable order of development of the micromesenteries and tentacles. *a–d*, micromesenteries lettered according to their probable order of development; *1–5*, tentacles.

megacœles there are three micromesenteries, of which the two adjacent to the macromesenteries are the longest, the middle one being distinctly shorter.

It can hardly be doubted that the longer micromesenteries are the older, the shorter the more recently formed. This rule holds good for all other Actinians, and there are no grounds for supposing that the Edwardsiæ form an exception to it. On the assumption that the rule is applicable to this case, my interpretation of the facts is given in the series of diagrams of a single megacœle (text-fig. 2, 2 to 5).

In 2 the megacœle has been divided peripherally into two microcœles by the formation of the micromesentery *a*. The primary tentacle of the original undivided megacœle is marked *1*, and the new tentacle *2* has grown out from the more dorsal microcœle. In 3 the megacœle has been subdivided into three microcœles by the formation of the micromesentery *b* ; the primary tentacle remains in the middle, and the new tentacle *3* has sprouted from the ventral microcœle. This is the condition found in all the dorso-lateral, lateral, and ventro-lateral megacœles in *E. rakaiyæ*.

In 4 a new micromesentery *c* has been formed on the dorsal side of the primary tentacle, and in connection with it the new tentacle *4* has been formed. In the next stage (text-fig. 2, 5) a new micromesentery *d* has been formed on the ventral side of the primary tentacle, and the new tentacle *5* has been formed in connection with it. This is the condition of the right dorso-lateral megacœle of specimen B and of both dorso-lateral megacœles of specimen C. The formation of two new micromesenteries, with their corresponding tentacles, one on the dorsal side and one on the ventral side of the primary tentacles, will produce the arrangement found in the left dorso-lateral megacœle of specimen B.

My examples A and C of *E. carnea* were not so fully expanded as example B, and their peristomes being crumpled it was not possible to determine the lengths of the micromesenteries with the same accuracy in sections ; but, so far as I was able to observe, they showed the same arrangement as has been described above.

In the ventro-lateral megacœles the order of appearance of the micromesenteries and tentacles is the reverse of that described for the dorso-lateral megacœles, and in the lateral chambers it appears that the first micromesentery may appear on the dorsal side of the primary tentacle, as in *E. claparedii*, or on the ventral side, as in *E. willeyana* and *beautempsii*.

It will be observed that the inferences drawn from the study of the length of the micromesenteries in a single species confirm in every respect the inferences drawn from the relative lengths and insertions of the tentacles in a number of other species of the genus *Edwardsia*.

Summing up the preceding argument, the law of the succession of the mesenteries and tentacles in the Edwardsiæ may be stated as follows :—

After the establishment of eight macromesenteries dividing the cœlenteron into eight megacœles, each of the latter is produced in the peristomial region into a single primary tentacle.

The two directive megacœles are never subdivided, and never prolonged into more than one tentacle.

In the capitulum the peripheral portions of the remaining megacœles are subdivided into microcœles by the successive formation of micromesenteries.

The micromesenteries appear singly, and usually in the following order on each side of the actinopharynx. First, a single micromesentery in the lateral megacœle ; then a single micromesentery successively in the dorso-lateral and the ventro-lateral megacœle. In some cases, however (*E. claparedii*), the micromesentery of the ventro-lateral megacœle is formed before that of the dorso-lateral.

Usually in the lateral and ventro-lateral megacœles the more dorsal of the two microcœles formed by the first micromesentery bears the primary tentacle, the more ventral the secondary tentacle ; but the opposite is the case in *E. claparedii* and probably in *E. mammillata*. In the dorso-lateral megacœle the primary tentacle is always in the ventral of the first two microcœles, the secondary tentacle in the dorsal.

Succeeding micromesenteries are formed singly and always on the side of the primary tentacle furthest from the last-formed secondary tentacle. As the microcœles and the tentacles into which they are prolonged are always formed first on one side, then on the other side of the primary tentacle, the latter always occupies a central or subcentral position in the megacœle.

The rate of growth is usually greatest in the dorso-lateral, next greatest in the ventro-lateral, and least in the lateral megacœle ; but in *E. claparedii* the rate of growth in the ventro-lateral megacœle seems to outstrip that in the dorso-lateral, and in some examples of *E. carnea* growth is most rapid in the lateral megacœles.

It is clear that, after the stage with eight mesenteries is reached, the sequence of mesenterial development in the Edwardsiæ differs altogether from that of the Hexactinians, and, indeed, from that of any known Actinian. The characteristic feature is that any two micromesenteries of the same age in any given megacœle constitute a *couple*—that is to say, they arise as singles on opposite sides of the actinopharynx, and not in *pairs* in the exocœles as in Hexactinians and Zoanthids. *Edwardsia* therefore retains the bilateral mode of growth throughout its existence, and exhibits no trace of the biradiality characteristic of the second stage of growth of the Hexactinians. In this respect it shows some analogy with the Cerianthidæ, but differs altogether from the latter in the fact that both the ventral and dorsal directive megacœles remain undivided throughout life, and increase of growth takes place on either side of the two directive chambers, and not in one of them. On the other hand, the persistence of the two directive chambers in an undivided state is a feature which the Edwardsiæ share in common with the Hexactiniæ and the Zoantheæ, and points to a fairly close alliance between the three groups. There is, further, some analogy in the mode of growth of Edwardsiæ and Zoantheæ, in that in both the addition of mesenteries after a certain stage proceeds more rapidly in certain megacœles ; but the Zoantheæ are

much more specialised in this respect than the Edwardsiæ. The outstanding feature, however, in the growth of the Edwardsiæ is that, after the eight-rayed stage is reached, the mesenteries continue to be formed in *couples of singles* and not in *couples of pairs*, as in the Dodecactiniaria and Zoanthinaria. In short, the mode of development characteristic of the first four couples formed in the larvæ of Zoantheæ, Actinians, and Madreporaria is continued to the end in Edwardsidæ. This mode of development is universally regarded as primitive. The Edwardsidæ, then, retain the primitive mode of development and growth throughout their existence and for this reason must be regarded as a separate branch of a primitive stock in which only four couples * of mesenteries were present. From this stock the Edwardsiaria, the Zoanthinaria, and the Dodecactiniaria have been derived.

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* Throughout this paper I have used the terms "couple" and "pair" in the sense indicated by Faurot. In my article on the Anthozoa in Lankester's 'Treatise on Zoology' I use the same terms, but in exactly the opposite sense to Faurot. My article, though published in 1900, was written in 1895, the same year in which Faurot's paper appeared. His use of the terms has priority over mine and should be adopted.

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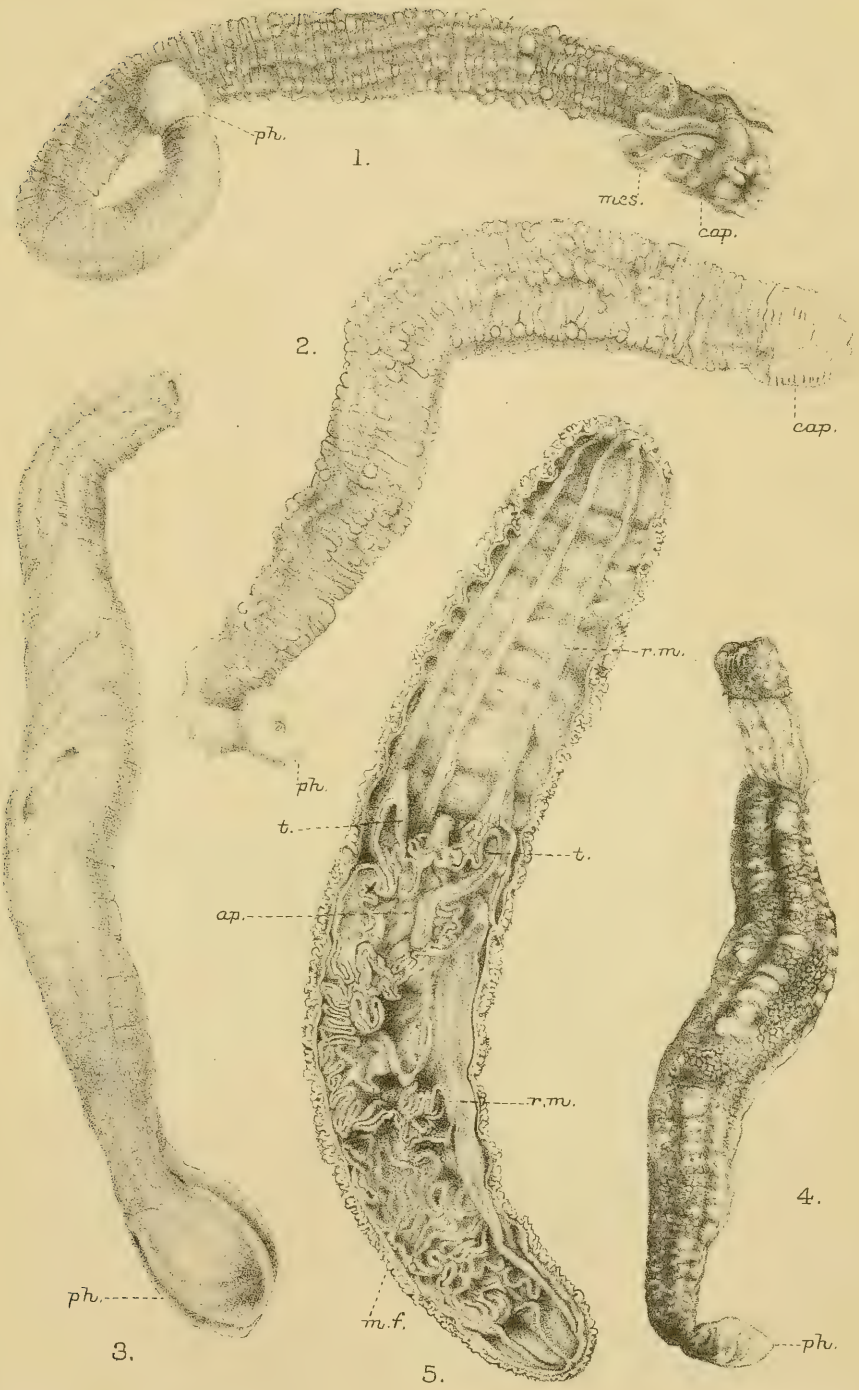
## EXPLANATION OF PLATE 51.

*cap.*, capitulum ; *ph.*, physa ; *mes.*, mesenteries.

Fig. 1. *Edwardsia mammillata*, n. sp. The specimen has burst below the capitulum, and the mesenterial filaments are extruded.
2. *Edwardsia rugosa*, n. sp.
3. *Edwardsia vermiformis*, n. sp.
4. *Edwardsia rakaiyæ*, n. sp. The animal has burst owing to excessive contraction in spirit, and the inner wall of the introverted part of the scapus is exposed in the upper part of the figure.
5. *Edwardsia willeyana*, n. sp. The retracted animal has been cut in half longitudinally, and the figure shows the tentacles *t.*, *t.*, the actinopharynx *a.p.*, the longitudinal retractor muscles *r.m.*, and the mesenterial filaments *m.f.* Owing to excessive contraction in spirit, the capitulum has been torn away from the scapus and has been pulled down to the inside of the lower half of the body.

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NEW SPECIES OF EDWARDSIA.